

Auditory bulla structure and relationships of the family Hyaenidae

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Abstract. Study of the structure of the auditory bulla in living and fossil hyaenids makes it possible to suggest that the double-chambered bulla of the Hyaenidae evolved from the archaic basicranium of stenoplesictine aeluroids separately from other Feliformia. The anterior chamber has a structure similar to that in Caniformia, and hyaenids then evolve a posterior chamber that is not homologous with the entotympanic chamber of other Feliformia. Whereas in the latter an intrabullar septum is formed mainly or solely by the ectotympanic, in Hyaenidae it is formed solely by the caudal entotympanic and the posterior chamber of the hyaenid bulla can be termed "pseudoentotympanic". The presence of the caudal entotympanic in the anterior part of the bulla and the absence of the ectotympanic in the intrabullar septum show that the family Hyaenidae is more closely related to the Nimravidae than to the living families of Feliformia.

Key words: Taxonomy, systematics, Mammalia, Carnivora, Hyaenidae.

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I. INTRODUCTION

The answer to the question "What is a hyaena?" has usually been sought in the morphology of the basicranium, auditory region, limb bones and dentition, or in the presence or absence of the alisphenoid canal and other features separating the families Hyaenidae and Viverridae. But an exact criterion for the separation of these families is lacking, because no single synapomorphy for all hyaenids has been found.

Unquestionably, only the morphology of the auditory bulla can provide a key to the separation of Hyaenidae and Viverridae. Study of the bulla structure in living and fossil hyaenids has shown that the differences in the auditory region in this family are much more significant than was previously supposed in the revision of the subfamily Ictitheriinae (SEMENOV 1989).

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II. DISCUSSION

According to the modern views (FLYNN et al. 1988; HUNT 1974, 1987, 1989; HUNT & TEDFORD 1993; WERDELIN & SOLOUNIAS 1991) the presence of a double-chambered bulla is a synapomorphy for all Feliformia and the main distinction between Hyaenidae and Viverridae consists in the placement (recumbency) of the intrabullar septum. The prevailing hypothesis is that the inclination of the *septum bullae* in a sequence of stages converts the viverrid bulla into the hyaenid one.

However, if this sequence is valid, the caudal chamber should primarily decrease in size (with inclination of the septum) from viverrids to "primitive hyaenids" and then secondarily increase (with the straightening of the septum) in true hyaenas in contradiction to the principle of parsimony. Moreover, the attribution of the aardwolf *Proteles cristatus* (SPARRMAN, 1783) to the Hyaenidae remains doubtful, since this species is not only highly autapomorphic in dental characters, but in bulla morphology as well.

In my opinion, differences between Hyaenidae and other Feliformia should be sought not in the recumbency of the intrabullar septum, but in the determination of which bones form this septum and the walls of the auditory chambers. Thus, in all Feliformia (except hyaenas) the auditory bulla is formed by three or four bones: ectotympanic, anterior and posterior caudal entotympanics (in the present paper these bones are considered as a single caudal entotympanic), and rostral entotympanic (HUNT 1974). Since the latter bone is not involved in the formation of the external walls of the bulla it is not considered further herein. The ectotympanic forms the anterior, ectotympanic, chamber of the bulla and the caudal entotympanic forms a posterior, entotympanic, chamber (Fig. 1C). These chambers are separated by the *septum bullae*. The septum is formed mainly by the ectotympanic, but it can be considered as partly bilaminar, since the inflected edge of the caudal entotympanic is involved in its formation. This is why the caudal border of the *septum bullae* is always situated at the margins (i. e., the junction) of the ectotympanic and caudal entotympanic and the posterior chamber of the bulla is always placed in front of the latter bone. The preferred method in the Feliformia to increase the volume of the middle ear cavity is by hypertrophy of the entotympanic chamber.

In Hyaenidae (except *Proteles*), in contrast to Feliformia, the whole external part of the bulla is formed by the ectotympanic chamber. This chamber is formed by two bones, ectotympanic and

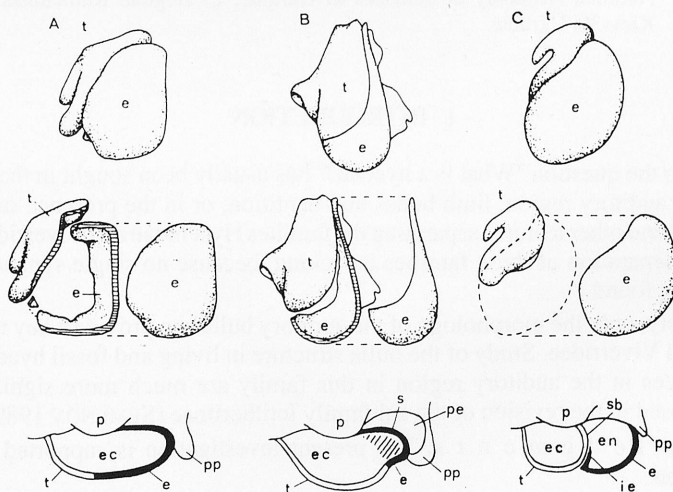


Fig. 1. Arrangement of the bones of their auditory bulla of aeluroid carnivores (ventral view and longitudinal section): A – *Dinictis*, B – *Crocuta*, C – *Felis*; e – caudal entotympanic, ec – ectotympanic chamber, en – entotympanic chamber, ie – inflected edge of caudal entotympanic, s – intrabullar septum of hyaenas, p – petrosal, pe – posterior (pseudoentotympanic) chamber of hyaenas, pp – paroccipital process, sb – *septum bullae*, t – ectotympanic; the shaded area in the ectotympanic chamber of *Crocuta* corresponds to the entotympanic chamber of Feliformia (compiled on evidence from HUNT 1974, 1987, 1989).

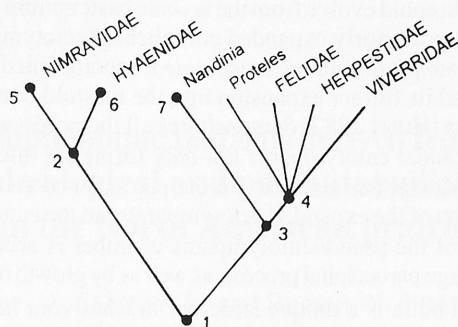


Fig. 2. Cladistic hypothesis of the aeluroid carnivores relationship. Characters defining the nodes are given in Table I. Node 1: 1b, 5b; Node 2: 2a, 3a, 6b; Node 3: 2b, 6a; Node 4: 3b, 4b; Node 5: 4a; Node 6: 4c; Node 7: 3a, 4a.

Table I

Selected character states of aeluroid carnivores. Abbreviations: FE – Felidae, HE – Herpestidae, HY – Hyaenidae, NA – *Nandinia binotata*, NI – Nimravidae, PR – *Proteles cristatus*, VI – Viverridae.

	Character states
1a.	Ventral promontorial surface of petrosal not produced into a ventral promontorial process that buttresses the basioccipital (arctoid and cynoid Carnivora)
1b.	Petrosal promontorium develops a prominent ventral promontorial process that buttresses the lateral margin of the basioccipital; the rostral entotympanic is situated anterior to the ventral promontorial process (NA, VI, HE, HY, PR, some NI, primitive FE)
2a.	Ectotympanic-caudal entotympanic junction does not show a tendency to form a <i>septum bullae</i> (NI, HY)
2b.	Ectotympanic-caudal entotympanic junction shows a tendency to form or forms a <i>septum bullae</i> (FE, VI, HE, NA, PR)
3a.	Caudal entotympanic forms a part of the external wall of the anterior bulla (NA, NI, HY)
3b.	Caudal entotympanic is not involved in the formation of the anterior bulla (FE, VI, HE, PR)
4a.	No internal septum (NA, NI)
4b.	<i>Septum bullae</i> is formed mainly by the ectotympanic (FE, VI, HE, PR)
4c.	The intrabullar septum is formed solely by the caudal entotympanic (HY)
5a.	PV4 without parastyle (Caniformia)
5b.	PV4 with parastyle (FE, VI, HE, HY, some NI)
6a.	The upper part of the braincase is more or less rounded with a sharply prominent plate-shaped sagittal crest (if present), the occipital crest is well developed and the frontal sinuses are not extended posterior to the fronto-parietal junction (VI, HE, NA, most FE)
6b.	The whole upper part of the braincase is wedge-shaped and the sagittal crest is never distinctly separated, the occipital crest is small and the frontal sinuses sometimes are extended up to the occipital bone (?NI, HY)

caudal entotympanic, without inflection of their margins to form a *septum bullae* (Fig. 1B). Such a structure of the external wall of the bulla is universal in Caniformia and this explains why the bulla of hyaenids was seen as single-chambered until POCKOCK (1916) discovered the posterior chamber. The whole intrabullar septum is unilaminar and formed solely by the caudal entotympanic. In other words, the posterior chamber of the hyaenid bulla is placed posterior to the caudal

entotympanic and cannot be regarded as homologous with the entotympanic chamber of other Feliformia. Thus, the posterior chamber of hyaenas can be named "pseudoentotympanic". Obviously, this type of auditory bulla could evolve from the archaic basicranium of stenoplesictine aeluroids through conjunction of the posteriorly expanded ectotympanic-caudal entotympanic bone with *apophysis paraoccipitale* and *pars mastoidea*, accompanied by formation of a chamber posterior to the petrosal and its further expansion into the mastoid bone and paroccipital process. A bulla like that of *Dinictis* (HUNT 1987) demonstrates all the necessary conditions for formation of the hyaenid bulla: the caudal entotympanic not only forms the internal and posterior walls of the bulla but also lines its dorsal part posterior to the petrosal and there is no tendency to form a *septum bullae* in the junction of the expanded ectotympanic and the caudal entotympanic (Fig. 1A). In hyaenids, hypertrophy of the pseudoentotympanic chamber is accompanied by its expansion into the mastoid bone and large paroccipital process, as well as by growth of the ectotympanic chamber.

Therefore, the hyaenid bulla is a unique structure in Carnivora indicating that this family is more closely related to the Nimravidae than to other Feliformia. Moreover, the Hyaenidae demonstrate a unique construction of the braincase. In most Feliformia the upper part of the braincase is more or less rounded, with a sharply prominent plate-shaped sagittal crest (if present), the occipital crest is well developed and the frontal sinuses are not extended posterior to the fronto-parietal junction. In Hyaenidae the whole upper part of braincase is wedge-shaped and the sagittal crest is never distinctly separated, the frontal sinuses are extended, sometimes up to the occipital bone, and the occipital crest is always small. It should be noted that in Nimravidae such as in *Dinictis* (HUNT 1987) the shape of the braincase is very similar to that in Hyaenidae.

As to the genus *Proteles* with its typical feliform structure of the bulla and unilaminar (ectotympanic) intrabullar septum, it can not be considered a hyaenid. There are many more reasons to accept the family Protelidae than there are to separate the Herpestidae from the Viverridae.

I hope that the characters discussed may provide strong nodes for phylogenetic analysis (Fig. 2), and that the proposed hypothesis will improve the situation with regard to the systematics of aeluroid carnivores. In particular, it might help to change the opinion of SCHMIDT-KITTLER (1976) that the percrocutoid hyaenids are distinct from other hyaenas and show derived characters in common with stenoplesictines. Moreover, the results obtained provide reasons why Hyaenidae together with Nimravidae are a monophyletic taxon and the sister taxon to Feliformia.

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